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THE AMERICAN NATURALIST

VOL. LIV.

July-August, 1920

No. 633

INHERITANCE OF CALLOSITIES IN THE OSTRICH

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"The problem of the method of evolution is one which the biologist finds it impossible to leave alone, although the longer he works at it, the farther its solution fades into the distance. The central point in the problem is the appearance, nature, and origin of the heritable varieties that arise in organisms."—H. S. JENNINGS.²

THE ostrich has a shield-like sternum devoid of a keel, a character it shares with the rest of the Ratitæ. The middle forms a broad, rounded projection, while the covering skin is greatly thickened, devoid of feathers, and constitutes a large, dense callosity on which the bird rests when crouching. Moreover, the ostrich is unique among birds in having a symphysis pubis, which forms a ventral projection behind corresponding with the one in front, only smaller, the skin over it likewise showing a strong callosity (Fig. 1). The result is that when the bird crouches the two median projections come into direct contact with the ground and the thickened pads support the greater part of the weight of the body, about 250 lbs., in front and behind, while it is steadied laterally by resting upon the upper surface of the nearly horizontal meta-

¹ The author is indebted to Dr. Raymond Pearl for seeing the paper through the press.

² *Journ. Washington Academy of Sciences*, Vol. VII, No. 10, May 19, 1917, p. 281.

tarsals and feet (Fig. 2). The sternal and pubic callosities may therefore be looked upon as a direct response of the skin to the pressure and friction of the body against the hard ground. Also in its frequent habit of

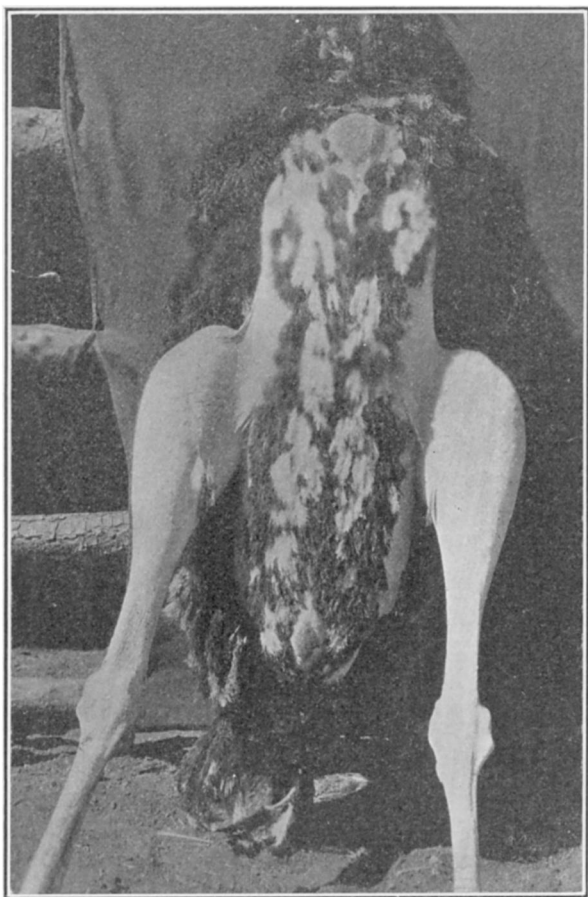


FIG. 1. Under surface of ostrich showing the large sternal callosity in front and the small pubic callosity behind. The darkened surface of both is due to the adherence of dirt. The bird is a young cock about eighteen months old in which the white ventral feathers are not yet completely replaced by black.

taking a "dust-bath" the ostrich rolls from side to side, the two projections being in the axis of motion, and this serves further to extend the area subject to pressure and friction.

In man and mammals generally a callosity usually con-

sists of a single, smooth or papillose thickened area of the skin, resting upon a bony support; but in the ostrich, as in other birds and in reptiles, it is constituted of a number of separate and distinct thickenings, somewhat regular in their arrangement, which give the appearance of a rounded or angular mosaic or tessellation (Figs. 5 and 6). This is typically shown on the under surface of the toes of birds and lizards, where the elements tend to

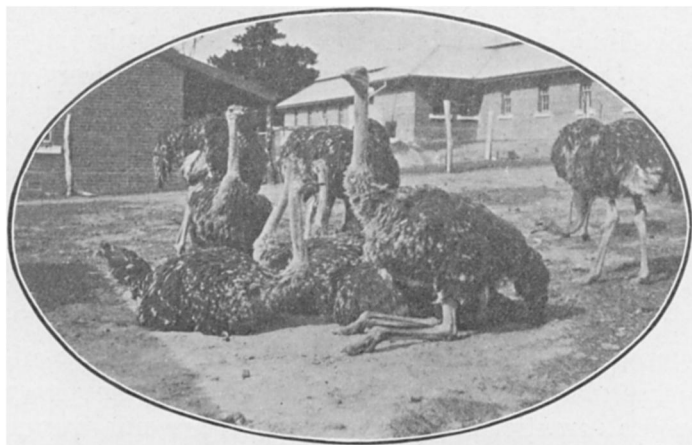


FIG. 2. Group of young ostriches, about six months old, the one in the foreground seen in a half-crouching attitude. The weight of the body is supported upon the inside of the ankle and the partly upturned two toes. When fully crouching the bird lurches forwards and comes to rest upon the sternal and pubic callosities, the tarsus and toes remaining in the same position.

be elongated and present a coarsely villous effect. Where the skin is scaly each callous constituent corresponds with an individual scale, but the latter has evidently no determining influence upon the form assumed, for the same tessellated arrangement is found over the sternal and pubic thickenings, though no scales are present. It is probable that the typical form of the reptilian callosity was first determined by the presence of the epidermal scales of the skin, and the latter still responds in the same manner in birds, not only on the legs and toes where scales occur, but over other parts of the body from which they are absent. The present interest lies in the fact that the characteristic form assumed by a callous area in the ostrich enables it to be sharply distinguished from the

surrounding parts of the skin which remain smooth. The tessellation, along with the thickening below, gives it a distinctive character as compared with the pads in mammals, which are mere thickening of the skin, and whose claim to be regarded as a "character" might at times be disputed. Where a callosity assumes any considerable thickness the underlying bone exhibits a correlated response by likewise becoming thickened, as is well shown on both the sternum and pubis of the ostrich.

The skin of all vertebrates appears to have the inherent power of responding to frequently repeated pressure and friction by the formation of thickenings over the bony projections upon which it rests. The pads are special protective adaptations to meet intermittent pressure and friction, upon what would otherwise be soft vulnerable parts of the body. They can arise at any part of the surface of the skin and may slowly disappear when the causal stimuli are no longer operative. Many of them are temporary responses, acquired during a part of the life-time of the individual, and come under the group of adaptive somatic modifications which are non-transmissible, though others, especially those on the under-surface of the feet, are transmissible and may therefore be regarded as germinal in their origin. *Thus similar characters, alike in structure and function, may be either individually acquired and non-transmissible or germinal and heritable.*

The ostrich resembles man and other animals in having the inherent power to produce special callosities over parts of the skin not usually subjected to pressure and friction, as the following observation proves. A chick was hatched in the incubator with its legs widely apart, in such a manner as to be incapable of supporting itself upright in the normal fashion. A deformity of this nature is not unusual among both ostrich and poultry chicks as a result of imperfect incubation, but can generally be rectified by bandaging the legs and drawing them nearer together for a day or two. In this instance however advantage was taken of the deformity to deter-

mine how far the skin would respond to unusual friction and pressure. With its legs widely apart, the chick naturally lay almost prone upon the ground, the inner side of the ankle constituting a feeble support, the tarso-metatarsus having here a projecting knob. The chick was able to raise itself slightly upon the latter and also to drag itself along the ground. It was kept alive for about ten days, and in that time developed a very conspicuous callous thickening over the inside of the metatarsal knob just below the ankle, the normal hereditary callosity along the back of the ankle being unused. The thickening was covered with the minute scales present over the leg generally, but the degree of friction was too intense and continuous for the skin wholly to adapt itself, and a slight abrasion occurred at the apex of the thickening, as in the human hand where pressure and friction are applied too continuously for the callous formation to keep pace with them.

The sternal and pubic callosities are not the only ones in the ostrich which appear to represent adaptive responses to the special habits of the bird. When taking its frequent sand-baths, it rolls about in the dry sand or dust, from side to side, and at the same time uses its wings in an oar-like manner. During the process the under surface of the latter is dragged over the ground and then turned upwards, inwards and backwards, scattering the sand or dust over the body generally, first from one wing and then from the other. The front or pre-axial border of the wing is necessarily subjected to much friction, and develops slight callous areas wherever the internal bones project. Further, the third digit of the wing, which is usually buried in the flesh, is occasionally found projecting freely from the under surface, and its tip naturally comes in for a good deal of rough wear as the latter is dragged along the ground. In response, it becomes knob-like and thickened, the surface showing the characteristic callous markings (Fig. 3). The free tip of the supporting phalanx is also knobbed.

Taking into account the responsive nature of the skin

along with the activities of the ostrich there appears no reason why the sternal, pubic and alar callosities should not be regarded as direct, structural responses to the pressure and friction to which these parts of the body are subject in the every-day activities of the bird. They could be understood as acquired, adaptive characters. The experiment given has served to prove, what would naturally be expected from experience with other animals, that the skin generally is endowed with the power

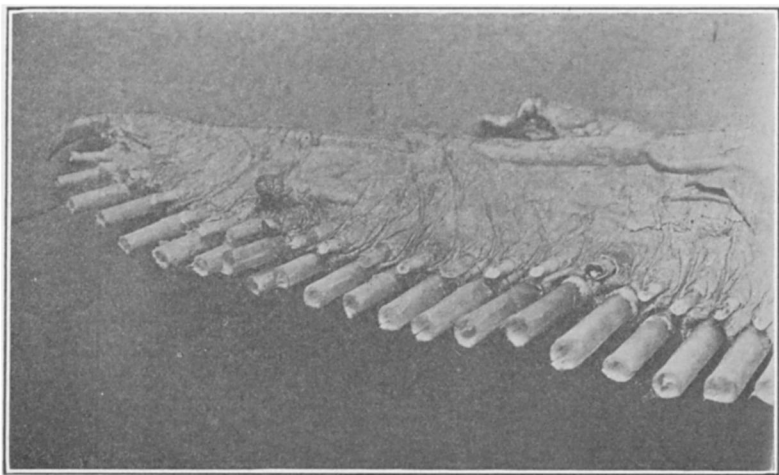


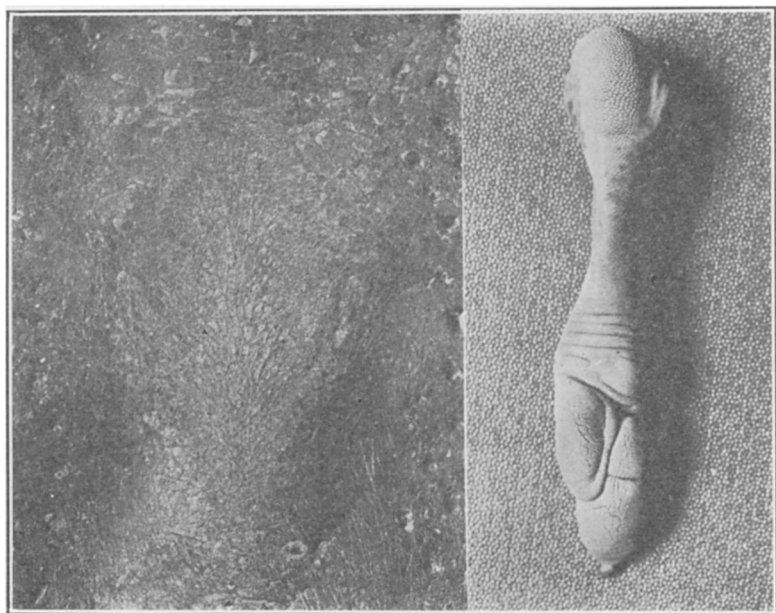
FIG. 3. Under surface of wing showing projecting third digit. The clawed ala spuria is seen above, the second finger is axial and also clawed, while the third projects freely from the under surface and is callous and knobbed.

to make callous responses when subjected to the necessary stimuli.

It was with some surprise therefore that in a series of embryos, representing all the stages passed through during the 42 days of incubation of the ostrich, the later ones were found to possess a perfectly developed callosity over both the sternum and the pubis, of exactly the same form and nature as in the young chick and adult (Fig. 4). The papillary outlines shown to be such a characteristic feature of sauropsidan callosities have the same variations in size and distribution as in the adult, and serve clearly to delimit the callous area from the remaining smooth

surface of the body. Examination of chicks from the time of hatching onwards leaves no doubt that the pre-natal callosities become those of the adult, the elevations becoming larger and coarser with use.

The rather insignificant callosities on the wing also show themselves on unhatched and newly hatched chicks.



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FIG. 4. Sternal covering of ostrich chick two or three weeks after hatching, showing the hereditary callosity fully established and functional. The cut ends of the feathers are seen surrounding the naked area.

FIG. 5. Callosities on foot and ankle of ostrich chick a few days before hatching. The thickenings are already well developed, the separate elevations on the toes being much narrower and closer than those on the ankle.

They are hardly distinguishable by any special thickening of the skin, but by the appearance of a faint reticulation in places corresponding with those in which they are found in the adults, and which serves clearly to separate them from the surrounding smooth surface. Even the tip of the third digit where sufficiently projecting shows a few markings, leaving no doubt they would later become the functional callosity.

We have therefore in the ostrich certain hereditary structural characters whose independent formation could in every respect be accounted for during the life-time of the bird from the known responsive nature of the skin and the habits of the creature. Examination of the adult alone and a knowledge of its activities would have justified us in regarding them as acquired adaptive characters, had not observation proved that they appear on the chick prior to hatching, and before the parts could have been subjected to the usual stimuli. *The ostrich has hereditary characters which could also be produced as adaptive responses to the habits of the bird.*

The old contentious question therefore arises as to whether the character first appeared as a response of the skin to the habits of the ostrich and has now become hereditary, or whether, having arisen fortuitously in the germ plasm, wholly apart from any adaptive need of the bird, it is now utilized by it. Has the habit developed the character until it has become transmissible or, the character being given, has it permitted of the adoption of the habit? The reply is simple and free from doubt: the callosity under any circumstances would develop *pari passu* with the habit and need of the bird, and neither the callosity nor the habit is dependent upon any antecedent formation. If the character did not arise in the first instance from the activities of the bird, subsequently becoming transmissible, it is manifest that it could originate by two distinct and independent methods, namely, from the germ-plasm and from post-natal stimuli.

It is not the first time that the presence of callosities in the embryos of animals provided with them in the adult has been adduced as evidence that characters originating during the life-time may be transmitted to the offspring. The best known case is that of the wart-hog, another African type—*Ex Africa semper aliquid novi*. With reference to this Professor J. Arthur Thomson³ remarks:

³ "Hereditry," London, 1912, p. 180.

The African wart-hog (*Phacochærus*) has the peculiar habit of kneeling down on its fore-limbs as it routs with its huge tusks in the ground and pushes itself forward with its hind-limbs. It has strong horny callosities protecting the surfaces on which it kneels, and these are seen even in the embryos. This seems to some naturalists to be a satisfactory proof of the inheritance of an acquired character. It is to others simply an instance of an adaptive peculiarity of germinal origin wrought out by natural selection.

In the latter part of the above quotation Thomson merely presents the two opposing views without affording us the advantage of his own. The last sentence is a succinct expression of present-day orthodoxy, and we may well consider how far it is justifiable in the case of the ostrich. It is manifest that from their very nature the callosities are outside the realm of competitive strife, and therefore could not have been "wrought out by natural selection." If a character is such that it must perforce be produced as a result of the every-day activities of an animal it is as wholly gratuitous to invoke natural selection as it would be to seek an independent germinal origin. As already shown, the skin of the ostrich is of such a nature that it will form callosities wherever friction and pressure are intermittently applied, just as surely as they will be produced on the human hand as a result of manual labor, on the finger tips of the harpist, violinist or rosary devotee, or on toes encased in ill-fitting boots, with all of which natural selection has no concern. Originally natural selection may have been operative in the survival of animals having the inherent power to form the thickenings, but we have abundant evidence that all the higher forms now possess it.

When the ancestral ostrich first took to resting on its sternum and pubis and rocking from side to side, the callous thickenings would arise quite apart from any antecedent formation and whether or not the germ-plasm had anticipated the need. An inherent power is transmitted, and nothing is gained by transmitting the callosities themselves, since they are adaptations which could arise in the natural course as needed. No selection

is involved in producing the "horny hand of toil"; it forms in the individual in proportion to the need for it. If fore-doomed to hard manual labor some advantage may possibly be conceived in having the callosities in advance, but would be insufficient to be of any selection value.

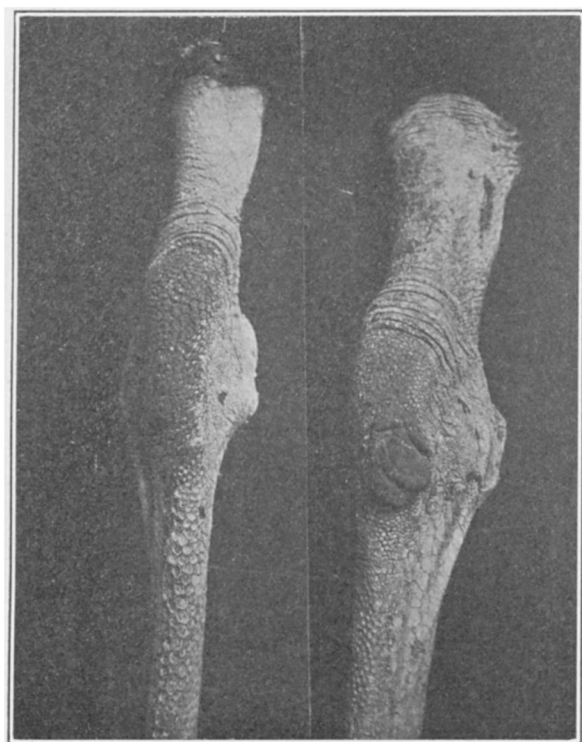
The position resolves itself as follows: From the known responsiveness of the skin of the ostrich to intermittent pressure and friction and the established activities of the bird it is just as certain that the sternal, pubic and alar callosities could be acquired in each generation independently as that similar thickenings could develop on the palm of the human hand engaged in labor. If we are not prepared to admit that the callosities first arose as somatic adaptations and then became hereditary, we have to face the alternative that at some time in the history of the ostrich a change took place in its germ plasm of such a nature as to give rise to a directly adaptive character, altogether similar to what could be somatically acquired; we have to admit that an exactly similar character could be produced in two wholly different ways: (a) directly as a response to the activities of the bird; (b) as a result of germinal changes. The same character could be somatically acquired and could arise germinally.

Of course the same argument could be applied to the strongly marked callosities on the toes and ankle of the ostrich which are also hereditary (Fig. 5). But these are not so peculiarly specific for the present purpose. Hereditary pedal thickenings occur in most animals, and even Darwin⁴ regarded the thickened sole of unborn infants as "the inherited effects of pressure during a long series of generations." The thickenings on the sternum, pubis and wings are confined to the ostrich, and therefore afford a more circumscribed case for discussion, hereditary transmission from any other type being placed out of consideration, though it is not unlikely that some of the other Ratites may have corresponding structures.

An acquired, non-transmissible, callous pad, presumably due to a change in the crouching habit of the ostrich

⁴ "Descent of Man," p. 18.

in the course of its phylogeny, remains to be noticed, as a further instance of the responsive power of the skin. Near the mesotarsal ankle-joint occurs a strong, elongated, hereditary callosity covering the median part of the broad, proximal end of the tarso-metatarsus (Fig. 5). This pad would naturally be used if the bird rested



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FIG. 6. Ankle region of young ostrich showing the symmetrical hereditary callosity above and the accessory one forming below on the inside (to the left).

FIG. 7. Ankle region of old ostrich in which the accessory ankle callosity (on the right) has become coarse and broken up.

squarely upon its tarsus and foot when crouching, the weight being mainly on the ankle. The ostrich however makes little or no use of it, for even in young chicks scarcely any evidence of contact with the ground can be observed. Somewhat to the inside there appears a new callous thickening, which begins to form by the time the chicks are a month or two old, and remains as the func-

tional pad throughout life, taking the place of the hereditary one which, though hardly used, persists structurally (Figs. 6 and 7). The new callosity is continuous laterally with the old median one, and altogether resembles it in character. No trace of it however appears in the chick prior to hatching (Fig. 5), hence it represents an individually acquired, adaptive character in the truest sense. We have therefore an original part of the ankle callosity which is hereditary, though now non-functional, and an acquired part which is functional and non-transmissible.⁵

The main facts presented seem capable of interpretation only in one of two ways: (a) *An acquired character which represents a structural response to stimuli resulting from the activities of the organism may become transmissible.* (b) *A character may arise germinally of a form and nature exactly similar to one which would otherwise be acquired independently from the known activities of the organism and the established responsive nature of its structural parts.*

⁵ Manifestly in the course of its phylogeny some change has taken place in the manner of crouching of the ostrich, for instead of resting squarely upon the median part of the ankle it has come to support itself mainly upon the inside. One ventures the suggestion that the change is to be associated with the loss of the second toe in the course of the retrogressive evolution of the foot. During a part of its phylogenetic history the ancestral African ostrich had unquestionably three toes like the living *Rhea*, the American three-toed ostrich, representing the second, third and fourth of the penta-dactyle series. The second has disappeared in the two-toed ostrich *Struthio*, though considerable traces exist in the embryo.

In its three-toed stage the ostrich would rest squarely upon its ankle, the other extremity of the limb being steadied by the upturned three toes, a smaller one on each side of the large middle third. A symmetrical median callosity would naturally form at the ankle-joint and, according to the view here maintained, would become transmissible. With the loss of the inner or second toe through degeneration the inside distal support for the tarsus would disappear, and the latter would tend to tilt inwardly along its whole length, in such a manner that the median part of the ankle would no longer support the bird. The callosity over it would be unnecessary, but a new one would form over the new area of support. In the ostrich of to-day the ancestral, hereditary ankle callosity, reminiscent of the three-toed stage, still appears, though functionless; a new non-hereditary one is acquired afresh with each generation and assumes the function of the old, becoming the ankle support for the crouching two-toed bird (Fig. 7). The whole forms a remarkable illustration of correlation between a phylogenetic change and an adaptive ontogenetic modification.

In adopting the first interpretation we depart from the generally accepted opinion of biologists of the present day and admit that an acquired character may become transmissible; in maintaining the second we are exercising a credulity unjustified by biological experience.

In the voluminous literature of evolution and heredity, case after case has been brought forward by advocates such as Lamarck and Herbert Spencer, claiming to be illustrations of the inheritance of acquired characters, and just as surely has it seemed possible to interpret them in some other fashion, as Weismann and others have insistently done. The fate which has befallen these should suffice to make the boldest hesitate in adducing yet another. It is the apparently unassailable character of the two opposing statements above which emboldens one in all diffidence to re-open "the interminable question" of the late Professor W. K. Brooks, that leader and inspirer of so much American philosophical biology. The peculiar justification for the present claim seems to be that, were the callosities of the ostrich not transmissible, they could be acquired just as effectively from the responsive nature of the skin of the bird; also that natural selection has no bearing on the question, for they are adaptive structures which the organism has the inherent power to produce as required.

According to Weismann (quoted from Walter⁶) three things are necessary to prove the inheritance of acquired characters: "*first*, a particular somatic character must be called forth by a known external cause; *second*, it must be something new or different from what was already exhibited before, and not be simply the re-awakening of a latent germinal character; and *third*, the same particular character must reappear in succeeding generations in the absence of the original external cause which brought the character in question forth." It is contended that all the circumstances surrounding the sternal and pubic callosities of the ostrich are in full accord with these three requirements.

When assuming that an acquired character has become

⁶ H. E. Walter, "Genetics," Macmillan & Co., 1913, p. 94.

transmissible it is usually held that in some mysterious fashion it has so impressed itself upon the soma that it becomes represented in the germ plasm by one or more factors, determinants or genes which are able to reproduce the same character in the next generation. The difficulties of conceiving this are so great as to convince most students of its impossibility. On the other hand we have to admit that we know little as to the means by which a germinal factor arises and gains its expression as a somatic character. Apart from the accessory chromosome in sex cells and the highly suggestive work of Professor T. H. Morgan and his associates on germinal *loci* in *Drosophila*, we only know of factorial representation by somatic expression. We are ignorant of the relationships between the two, and of the measures by which one gives rise to the other. Were it not that Thomson has shown the contrast to be hardly justifiable, one would be inclined to ask: Is it not as difficult to understand how a genetic factor arises and comes to have somatic expression as it is to conceive how germinal representation may be gained by an acquired somatic character? We accept the one without demur, but are prone to deny the other as impossible. We must not forget the warning of Professor Lloyd Morgan that because the phenomenon of acquired transmissibility can not be understood it is not necessarily rendered impossible.

In considering the difficulty in the way of an acquired character gaining factorial representation in the germ plasm it is legitimate to enquire whether a transmissible character is necessarily germinal as present-day teaching so consistently affirms, that is, whether it is necessarily represented in the germ plasm by definite genetic factors.⁷ We have admitted that we know little or nothing

⁷In a sense everything appearing in the soma may be regarded as derived from the germ, but the factorial hypothesis has given us a clear understanding as to what is meant when we say that a character is germinal. With the question of acquired characters before us there need be no confusion as regards a germinal and a non-germinal character, and whether the latter appears pre-natally or post-natally. On the considerations here set forth a transmissible character is not necessarily represented directly by germinal genetic factors.

ing of the manner in which factorial representation in the germ plasm gains expression in the soma; on the other hand we have some experience, from observation and experiment, of the production of somatic changes in the life-time of the organism, as a result of environmental influences and of stimuli due to the use and disuse of parts. The production of callosities, the variation of muscles and the skeletal changes in correlation therewith, the direct modification of bones, ligaments and mesenteries, are all adaptive changes which may result as responses to the external and internal stimuli to which the organism is subject during its life-time.⁸ They reveal the inherent powers of responsive adaptability present in the tissues and organs of the body. They are in truth characters which arise independently of direct representation in the germ plasm, and indicate that the latter is not the *fons et origo* of all structural changes. The power of the tissues to respond to stimuli is transmissible; irritability, the power of responding to stimuli, is one of

⁸ In a series of papers appearing in the *Journal of Anatomy and Physiology* from 1886 to 1888, Sir W. Arbuthnot Lane presents a remarkable series of adaptive changes which take place in the human body as a result of continued occupational activities. They are probably the fullest and most complete studies of this nature which we possess. One contribution, "A remarkable Example of the manner in which Pressure-Changes in the Skeleton may Reveal the Labour-History of the Individual," is a full account of the changes which appear in the skeleton of the coal-trimmer. The most notable feature is the formation of an arthrodial joint in the fibro-cartilage between the fourth and fifth lumbar vertebræ and the division of the neural arch of the fourth at two points, a result of the forcible rotation of the spine on a vertical axis which takes place when coal is thrown with great force to a considerable distance, as when the coal-trimmer is engaged at his work on board ship.

A second paper, "The Anatomy and Physiology of the Shoemaker," describes the anatomical and osteological changes which had resulted from the habitual performance of a definite series of movements entailing the expenditure of a considerable amount of muscular energy, during the greater part of a long life-time of seventy-three years. The most striking change is the formation of a buttress of bone, which extends upwards from the lateral mass of the atlas on the one side, and articulates by means of an arthrodial joint with the jugular process of the occipital bone.

Along with other papers dealing with more or less cognate subjects the two are included in a single volume under the non-suggestive title, "The Operative Treatment of Chronic Intestinal Stasis," J. Nesbet & Co., London, 3d ed., 1915.

the fundamental attributes of protoplasm. The manner of the response is adaptive, it is an individual effort, and is usually non-transmissible. Whether the responses ever become transmissible, in that they appear without the original stimulus, is the crucial point of the problem of the transmission of acquired characters. That the organism has the inherent power of forming new non-germinal characters is however not questioned, and it is well that the hard fact should be kept in mind. What we desire is some evidence that stimuli are transmissible or, if this be not forthcoming, some proof that the responses may appear without the original stimuli. At first this may be deemed to be looking for an effect without a cause, a response without a stimulus.

The callosities in the ostrich and adaptive responses generally lead one to submit that a character may become transmissible without necessarily being germinal, in the sense of having factorial representation in the germ plasm. Acquired characters are such somatic modifications as are produced as responses of the organs and tissues to stimuli, and are without direct representation in the germ plasm. In the words of Weismann: "Acquired characters are those which result from external influence upon the organism, in contrast to such as spring from the constitution of the germ."⁹ They reveal an inherent power of response of the tissues and organs in a more or less definite manner according to the differentiation of the tissues and the nature of the stimulus. It may be that much of the complicated development of to-day was primarily of the nature of responses to stimuli.

The acceptance of Weismann's germ plasm theory of inheritance, strengthened as it has been by the factorial hypothesis, has for the past two or three decades concen-

⁹ Professor J. A. Thomson's definition ("Heredity," 1912, p. 173) is as follows: "An acquired character, or a somatic modification, may be defined as a structural change in the body of a multicellular organism, involving a deviation from the normal, directly induced during the individual lifetime by a change in the environment or in function (use and disuse), and such that it transcends the limits of organic elasticity, and therefore persists after the factors inducing it have ceased to operate." Among his illustrations he cites: "callosities induced on the skin by pressure."

trated attention wholly on the germ plasm as the source of heredity and variation in the animal world. Ordinarily in studying the origin of characters we start with the germ and consider how factors arise and characters come to be formed from them; but there is no reason why we should not also contemplate their origin by observing their manner of appearance in the soma, and from this try to understand their transmissibility. Even if hitherto the former has alone proved fertile in results and the latter sterile it does not follow that renewed attacks on the problem with additional armament will always fail.

Callosities are a definite response of the skin to stimuli resulting from contact with some hard substance involving pressure and friction. They involve new inter-relationships of the structures concerned, and may affect the underlying tissues and even the bone on which they rest. On the factorial hypothesis the multitude of characteristics making up the complex organism are assumed to have a measure of independence; yet it is allowed that definite hereditary inter-relationships exist among them when we contemplate the body as a whole. May not some of the characteristics be directly factorial and others a result of the inter-relationships brought about in their establishment, just as in architecture certain subsidiary structural parts have to be introduced in order to admit of some major effect.¹⁰ In any structural change, however simple, and whether germinal or somatic in origin, the complex tissue inter-relationships of the organism are involved. The old ties are disturbed and new ones are established. It is conceivable that a continuance of the application of fresh stimuli, from generation to generation, may result in a weakening of the old relation-

¹⁰ Mr. L. Doncaster ("Heredity," Cambridge, 1911, p. 97) expresses much the same idea when he says: "The belief that 'somatic' changes could not be transmitted rests largely on the idea that every character is determined by a 'factor' or determinant in the germ-cell, but it is clear that any character is not developed directly from the germinal determinant, but by the relation existing between the determinant and its surroundings, viz., the body of the organism. If the surroundings are changed, this relationship may be altered, and the altered relation may be transmitted to the offspring, so bringing about a corresponding change in the character as it appears in the next generation."

ships and a strengthening of the new, until in the end one may supplant the other.

On a hypothetical conception of this kind it may be understood that the continued production of sternal and pubic callosities, generation after generation, has introduced such fixed and intimate inter-relationships of the structural parts concerned that in the end they come to replace the old inter-relationships altogether and with them the non-callous condition. The callosities are formed antecedent to and apart from the primary stimuli. Their appearance becomes accelerated, as it were, and they arise even before the chick is hatched and the original stimuli can be effective. They are not new characters which have come in, but are new as regards the ontogenetic time at which they appear.

The possibility of responses occurring without the original normal stimuli may be illustrated from certain of the instinctive sexual activities of the ostrich. At the breeding season the cock bird performs the sexual display known as "rolling." He crouches on the ground and with wings outspread rolls from side to side, his long neck and head also taking part, the latter striking vigorously against each side of the body alternately. Also as he approaches sexual ripeness he begins to "bromm," the sound having often been compared with the roar of a lion. The mouth being closed he inflates the esophagus until the neck as a whole becomes two or three times its usual thickness and then forcibly expels the air through the nasal passages, producing a booming noise of great carrying power, consisting of two short notes and a long one, the sequence being repeated from one to six or seven times, and serving as a guide to the farmer as to the state of sexual ripeness of the bird. Again, during actual pairing, the cock mounts upon the back of the crouching hen with his right foot upon her back and the left upon the ground, and sways the front part of the body and neck to and fro as the act is consummated.

The above are three distinctive actions on the part of the cock ostrich which are usually performed only at sexual maturity, and may be deemed to be responses asso-

ciated with stimuli from secretions or enzymes of the sexual organs. Yet occasionally very young chicks, perhaps only a week or two old, are to be seen performing the same, though in an imperfect manner. They can "roll" almost perfectly; a chick can inflate its neck, but has insufficient strength to expel the air with enough force to produce a "bromm"; and often one chick will attempt to mount another which is resting on the ground, and begin to sway from side to side in a ridiculous fashion. May not these precocious activities be interpreted as an acceleration of responses normally due to stimuli of a sexual nature? Now they are performed wholly apart from the usual stimuli and are of no adaptive nor selection value at this early stage. They have become, as it were, so integral a part of the organism that they break out without the original stimulus; they have become transmissible. They are hardly sufficiently general to be comprised under the term "play" and, in the sense of Carl Groos, to be regarded as preparatory to the real business of life. Probably many activities of a similar precocious nature could be brought forward where an intensive study of an animal has been made. They serve to show that a physiological action is not necessarily a response to the stimuli which originally called it forth; but may appear antecedent to and independently of them.

Just as physiological activities may make a precocious or accelerated appearance so it may be that acquired, morphological characters at times appear in advance and apart from the stimuli which originally called them forth; they may become transmissible, though not germinal in the factorial sense. It is submitted that the formation of callosities, ordinarily developed as responses to pressure and friction in the life-time of the individual bird, has become thus accelerated, so that they arise at a much earlier period, even within the egg, and apart from the usual stimuli. Arising in this way a character is not germinal in the sense of having factorial representation, but is nevertheless transmissible. Though appearing before hatching it is no more germinal than it would be if developed as a definite response to the post-natal stimuli

of friction and pressure. On this interpretation a new character, to wit, a callosity, can arise either before or after hatching as a result of the responsive nature of the tissues, apart from any germinal representation.

Acquired adaptive characters, structural responses to internal or external stimuli, are by their very nature extra-germinal, and their appearance may well lead us to hesitate in accepting the germ plasm theory as a complete interpretation of everything somatic, or of everything that is transmitted from generation to generation, despite the statement by Dr. C. B. Davenport¹¹ that: "Upon one point all geneticists are, however, agreed . . . that we must interpret all our results in terms of genes alone."

So plastic and so responsive are the parts of the organism to stimuli that, in spite of such an embrasive pronouncement, it may still constitute a subject for enquiry whether many of the adaptive relationships in organisms are not such as were originally impressed upon the individual as a result of its activities or subjection to former stimuli and which have in time become transmissible. The problem has been neglected for the past two or three decades as a result of the firm hold which the germ plasm theory of inheritance has gained over the minds of biologists and the general acceptance of the non-heritability of acquired characters. *Renewed search will probably disclose many other instances of characters appearing pre-natally which could just as well be developed as needed in the life-time of the individual, and thereby throw suspicion upon their germinal origin.* Callosities are undoubtedly the most direct and simple instances of this nature which could be adduced; we have both transmissible and non-transmissible examples in the same individual. Those whose transmissibility is established could have been formed post-natally just as readily as those produced where pressure and friction are applied to surfaces not already callous. Knowing also the responsive nature of muscles, tendons, ligaments and osteological tuberosities and the readiness with which they are modified through change of habits, it is not improbable

¹¹ AMERICAN NATURALIST, Vol. 50, August, 1916, p. 463.

that many now regarded as transmissible could also arise as needed as direct responses. It will certainly be legitimate to question the germinal origin of those characters whose formation can be interpreted as adaptive responses to changes to which the organism is subject.

The germ plasm theory of Weismann and the factorial hypothesis of Mendel, Bateson and others have been of inestimable value in enabling us to appreciate many of the facts of heredity. But no one imagines that they give us the completed account of evolution and adaptation, as many are beginning to feel now that their contributions can be estimated more or less in their entirety, and we get a true perspective of what they have to offer. They are and will remain important chapters in the story of variation, heredity and evolution, but they are not the whole volume; nor are they the concluding chapters, as their supporters themselves would doubtless admit. It is submitted that something is yet to be gained from consideration of how adaptive characters arise as a result of stimuli from use and disuse of parts and from environment, and how they may become transmissible, though not necessarily germinal. The germ plasm theory to a large extent and the factorial hypothesis *in toto* are sterile when we come to questions of adaptation, and natural selection has to be freely invoked, whereas practically every structure in the body bears witness to its adaptive nature.

For an acquired character to become transmissible, so that it appears independently of the stimuli which originally called it forth, is manifestly a difficult proceeding when regarded from the point of view of the hereditary structural relationships which have been established through long ages. The natural and experimental phenomena of regeneration show how deep is the tendency to maintain the established relationships of the various parts of the body. An acquired character represents some temporary disturbance of the normal relationships, but ordinarily the old correlations return with the next generation and the new are but transient, persisting for the generation only. When however these

new relationships are repeated generation after generation and maintained at their full vigor for the whole lifetime, it is conceivable that they become so impressed on the organism that they gradually overcome the old weakening relationships of parts and appear from the beginning in place of them, in other words, the character becomes transmissible, the new ties become the heritage of the organism. This, of course, is no proof of the inheritance of acquired characters, but may help us to conceive its possibility in the light of considerations engendered by the callosities in the ostrich.

The skin is more likely to show responses to environmental stimuli and to the general activities of an animal than the internal organs on account of its superficial, exposed position, and callous pads are among the simplest of structural responses and their formation is readily understood. Where temporary, as on the human hand, they are by no means likely to impress themselves permanently as new interrelationships on the surrounding parts. Where, however, as in the ostrich, they would form from the beginning and persist throughout life, from generation to generation, it is more conceivable that they would impress themselves on the constitution of the bird and their time of appearance would undergo acceleration with an independence of the primary stimulus.

The accessory, non-transmissible callosity at the ankle has not yet impressed itself so forcibly upon the general structural relationships as permanently to disturb the normal tendencies, and it has to be formed anew in each generation from direct stimuli. The hereditary median thickening is the primary one, and may well justify us in thinking that the three-toed, ancestral stage of the ostrich was of long geological duration; the new pad formed by the two-toed bird is more recent and has failed as yet to attain transmissibility. It may be that in its early days a race is more responsive to adaptive, structural changes than at a later period. In many respects the ostrich now appears senescent, and may well be expected to be less plastic than in past ages.

In general, correlated structural relationships, established through long ages, will act as a *vis inertiae* to the introduction of acquired changes; they will represent so much heritable, inherent tendency which has to be overcome before any new relationship of parts can be established. Life-time changes of habit or of environment, as in the assumption by man of the erect habit, or the taking to water of a former terrestrial organism, are the conditions which will be conducive to acquired changes becoming transmissible, compared with those under which the responses are temporary, or continued for a few generations, or are the result of mutilation.¹² Any temporary structural relationship established, as in the decaudation experiments of Weismann and others, would manifestly be incapable of overcoming those deeper relationships which, with each new generation, find their expression in a complete tail. As Professor T. H. Morgan¹³ points out, the theory of the inheritance of acquired characters "is one that has the great merit of being capable of experimental test," but he allows that "modern Lamarckians are justified in claiming that the validity of the theory can only be tested by experiments in which the organism is subjected to influences extending over a considerable period." The hypothesis here submitted is undoubtedly one which in most experimental cases would demand long period for the effectiveness of its tests.

We need not expect mutilations to become transmissible, nor most of the responses established during the life-time of an individual; but this in no way precludes the possibility for life-time responses which are continued for generations, or which may happen to strike a race at some plastic period of its existence.

¹² In the adoption of a new habit during the life-time an adaptive character may appear from generation to generation as the habit comes to be assumed, and give the appearance of being transmissible, whereas it may be formed as an ordinary response to the new stimuli. Especially where an animal is in process of changing the stimuli to which it is subject will it often be difficult to distinguish a transmissible from a responsive adaptive character which is non-transmissible.

¹³ Morgan, T. H., "Evolution and Adaptation," 1903, p. 230.

It is by no means anticipated that the conception of the transmissibility of characters as so many accelerated adaptive responses, involving new structural inter-relationships, and not necessarily with factorial germinal representation, will apply to all the features of an organism and serve as an explanation of the origin of heritable characters generally. Its application may be limited to such as have an adaptive significance, and can be assumed to have arisen in the first instance as a result of internal or external stimuli acting upon the soma. As will be shown in a later paper the ostrich itself, especially in the details of its degeneration, presents us with many character changes which have manifestly no adaptive significance, but are the expression of germinal changes, uninfluenced by external forces. Without question we are short-sighted in attempting to reduce the methods of evolution to some common term; as Professor H. F. Osborn points out in his new book: "The Origin and Evolution of Life,"¹⁴ there are *centripetal* factors in organic evolution, there are *centrifugal* factors. Much of the recent work on Mendelism and mutation strongly supports the view so warmly advocated by Professor W. Bateson and Professor T. H. Morgan that germinal characters appear apart from any adaptive considerations, and the degenerative changes in the ostrich are in full accord with this; but it is by no means a complete answer to the problems of evolution, where so much appears that is directly adaptive and so little that is non-adaptive. Most genetical work during the present century has been unconnected with adaptation, yet it is one of the big problems of biology which calls for solution as insistently as ever, and it may be that a proper interpretation of the callosities in the ostrich will assist in some measure towards an understanding.

¹⁴ Reviewed by Professor Lillie in *Science*, November 8, 1918.